

Figure 2

Mean individual burrowing time (sec) versus length (mm) for west (W) and south (S) coast populations of *Donax serra* at three experimental temperatures. ○ west coast; ● south coast.

species including two species of *Donax*. BRI for these species ranged from 0.01 to 20; species with a BRI greater than two were classified as rapid burrowers and greater than six as very rapid burrowers. *Donax denticulatus* and *D. variabilis* scored 17 and 7, respectively, on this scale. Recently, TRUEMAN & BROWN (1989) have given a BRI for west coast *D. serra* of 6.9. This corresponds well with the BRI's determined in this study, which span the range determined for the other two *Donax* species, indicating that *D. serra* is one of the most rapid burrowers of all species of bivalve examined to date. Furthermore, we have shown that the BRI is influenced by temperature. When comparing BRI's, care must be taken to state whether the measurements were done at ambient environmental tem-

peratures (ecological differences) or at constant experimental temperatures (physiological differences).

MCLACHLAN & YOUNG (1982) found that summer acclimated *Donax serra* burrowed more slowly at 10°C than winter acclimated animals, indicating seasonal acclimation in south coast populations. In light of this we expected that either both populations would burrow at the same rate, i.e., no adaptation, or that the west coast population would have adapted to the colder temperatures and burrowed more rapidly. Our results show that west coast populations burrow more slowly than south coast populations when acclimated to the same temperature.

One possible explanation for differences in burrowing time may be differences in shell morphology. Both shell obesity (width-to-height ratio) (TRUEMAN *et al.*, 1966) and shell elongation (STANLEY, 1970) have been shown to affect the rate at which bivalves burrow. Preliminary results indicate differences in shell morphology between south and west coast populations of *Donax serra*. These differences and their effect on behavior will be investigated in sub-

Table 1

Comparison of burrowing time vs. length regressions for south and west coast populations of *Donax serra* at three test temperatures. * $P < 0.05$.

	Intercept	Slope	r^2	n
T = 10°C				
South coast	-2.312	0.904*	0.683	32
West coast	-8.791 ^{n.s.}	1.234	0.790	30
T = 15°C				
South coast	-1.672*	0.428	0.643	50
West coast	11.512	0.387 ^{n.s.}	0.497	36
T = 20°C				
South coast	-0.926	0.459	0.697	33
West coast	2.490 ^{n.s.}	0.474 ^{n.s.}	0.707	29

Table 2

Comparison of burrowing rate index (BRI) of south and west coast populations of *Donax serra* at three temperatures. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Temperature	South coast	West coast	Significance level
10°C	6.35	5.22	**
15°C	13.85	8.97	***
20°C	12.52	10.42	**

Table 3

Comparison of burrowing times (seconds) for three size classes of summer and winter acclimated *Donax serra* from the south and west coasts. Data for summer acclimated animals taken from MCLACHLAN & YOUNG (1982).

Coast	McLachlan & Young (1982)		Present study	
	S summer (21°C)	S winter (16°C)	S winter (15°C)	W winter (15°C)
Test temperature	20°C	10°C	10°C	10°C
Length (mm)				
15	9	16	11	10
25	13	23	20	22
50	23	35	43	53

sequent papers. Similarly, TRUEMAN & BROWN (1989) found that *Bullia digitalis* from the west coast burrowed more slowly than individuals from south coast populations, but ascribed this to differences in physiological condition.

Water temperatures along the west coast are considerably colder than along the south coast (CHRISTENSEN, 1980). In addition, west coast populations of *Donax serra* burrow more slowly than south coast populations at the same temperatures. Therefore, in their natural habitats, the two populations will differ markedly in burrowing rate (Table 3). As both coasts experience similar wave climates (ROSSOUW, 1984), swash periods and frequencies should be similar. MCLACHLAN & YOUNG (1982) estimated that burial times must be less than 48 sec to prevent *D. serra* from being dislodged by subsequent swashes. Clearly, south coast populations can burrow sufficiently fast to maintain their position on the beach face, whereas the west coast populations would not have sufficient time to burrow at the peak of the swash before being carried down the beach by the backwash. This is indeed the pattern reflected in their observed field distributions; *D. serra* in the south coast inhabit the intertidal zone (MCLACHLAN *et al.*, 1979; DONN *et al.*, 1986), while on the west coast they are found at or below spring low water (HUTCHINGS *et al.*, 1983).

We conclude that there is little evidence for physiological adaptation of burrowing time to temperature between south and west coast populations of *Donax serra* and suggest that the lower than expected burrowing rates of the west coast population may be a result of morphological differences between the two. Furthermore, the combination of slower burrowing rates and lower environmental temperatures may be responsible for differences in zonal differences on the shore.

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Chemoautotrophic Sulfur Bacteria as a Food Source for Mollusks at Intertidal Hydrothermal Vents: Evidence from Stable Isotopes

by

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Abstract. Stable carbon and nitrogen isotope measurements indicate that limpets (*Lottia limatula*), which normally graze on algae, have diets consisting predominantly of chemoautotrophic sulfide-oxidizing bacteria at southern California intertidal hydrothermal vents. Suspension-feeding mussels (*Mytilus edulis*) at the intertidal vents show only minor inclusion of the chemoautotrophic bacteria in their diet. This is the first evidence from stable isotopes that geothermally driven primary production can be of major importance to intertidal grazers.

INTRODUCTION

The discovery of dense animal and bacterial populations at deep-sea hydrothermal vents, living in the absence of sunlight, suggested that these biological communities were supported locally by chemosynthetic vent bacteria rather than minimal amounts of photosynthetically produced material drifting down from the sunlit zone. Much evidence has since been gathered confirming the hypothesis that chemoautotrophic bacteria are the primary producers at deep-sea vents. These bacteria support a community of invertebrate grazers (*e.g.*, limpets), suspension feeders (*e.g.*, clams, mussels), predators and scavengers (*e.g.*, crabs), and may also supply organic carbon to macroinvertebrates through symbiotic associations (RAU, 1985; HESSLER & SMITHEY, 1984; CAVANAUGH, 1983; FELBECK & SOMERO, 1982; WILLIAMS *et al.*, 1981).

Vent bacteria produce biomass and obtain energy from oxidation of geothermally reduced compounds (*e.g.*, hydrogen sulfide, ammonia, and hydrogen) in vent waters (JANNASCH & WIRSEN, 1979). Sulfide-oxidizing bacteria appear to be among the most conspicuous primary producers at vents (RUBY *et al.*, 1981). Consumption of sulfide-

oxidizing bacteria occurs wherever sulfide levels are high enough to support chemosynthesis. In most of these habitats, however, the sulfide is biologically produced by sulfate-reducing bacteria (SPIES & DESMARAIS, 1983) rather than being geothermally produced as in deep-sea vents. The possibility that geothermally driven chemosynthesis is important for some organisms in habitats other than deep-sea vents has been suggested. STEIN (1984) reported the partial contribution of sulfide-oxidizing bacteria to the diet of black abalone *Haliotis cracherodii* Leach, 1814, at coastal hydrothermal vents. Ciliates, flagellates, and aquatic insect larvae consume sulfide-oxidizing bacteria in terrestrial hot springs (LACKEY *et al.*, 1965). Thus, geothermally driven primary production is not unique to deep-sea vents, and may contribute to community biomass wherever hydrothermal vents occur in the photic zone.

Little is known of the relative nutritional importance of chemosynthesis versus photosynthesis at sunlit vents. STEIN (1984) observed that in addition to black abalone, several species of limpets appeared to graze on benthic mats of bacteria (the most conspicuous species of the bacterial assemblage resembled *Thiothrix* Winogradsky, a known sul-

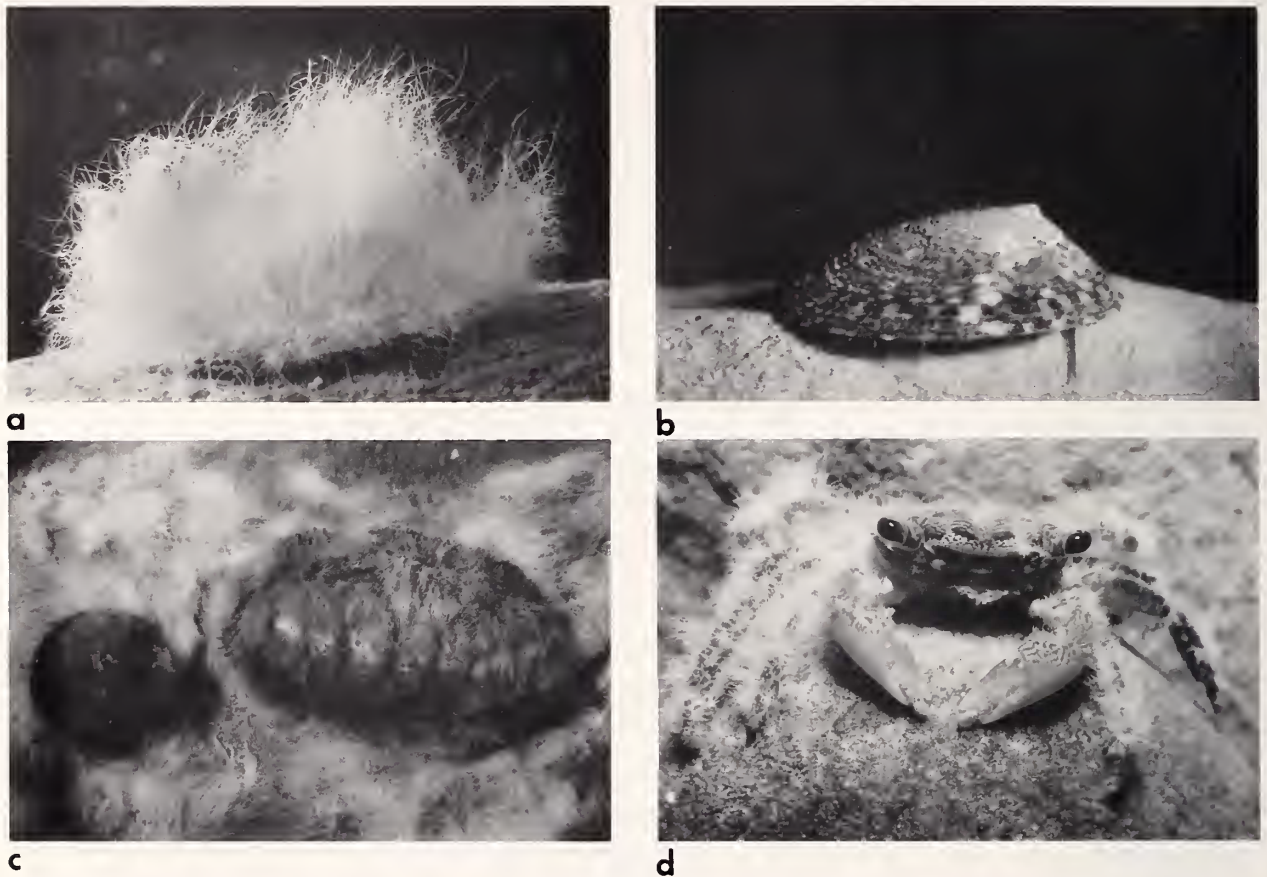


Figure 1

a. File limpet *Lottia limatula* from intertidal vent, with dense growth of filamentous sulfide-oxidizing bacteria on shell. b. File limpet collected 10 m from nearest vent. c. Mossy chiton *Mopalia muscosa* (Gould, 1846) and black turban snail *Tegula funebralis* (A. Adams, 1855) on bacteria-covered rock at intertidal vent. d. Shore crab *Pachygrapsus crassipes* from intertidal vent, with bacterial growth on exoskeleton.

fide oxidizer) at intertidal hydrothermal vents located at White Point, southern California. In our study, closer examination of intertidal vents in the same area where STEIN (1984) worked subtidally revealed the presence of numerous common intertidal mollusks and crabs. The hard body surfaces (shell and exoskeleton) of many individuals at these vents were covered with a thick growth of attached filamentous sulfide-oxidizing bacteria (Figure 1). These bacteria grow only in the immediate vicinity of vents where sulfide levels are high enough to support chemosynthetic production of biomass, and indicate that animals covered with bacteria spend a considerable amount of time bathed in the warm, sulfide-rich vent effluent (up to 28°C and 141 $\mu\text{M/L}$; STEIN, 1984).

These observations suggested that vent bacteria might form a substantial portion of the diets of some intertidal macroinvertebrates. We examined this possibility for two species of intertidal mollusks that occur commonly at and away from vents. The file limpet *Lottia limatula* (Carpen-

ter, 1864) is a benthic grazer, while the common mussel *Mytilus edulis* Linnaeus, 1758, was chosen as a representative suspension feeder.

MATERIALS AND METHODS

Possible dietary sources were investigated by measuring the stable carbon and nitrogen isotopic composition ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios) of both animal tissues and their potential food items. This approach was used because, if stable isotope ratios of different food types differ substantially, these isotopic ratios can be used as natural markers to trace dietary sources, as the ratios change little when assimilated into animal tissue (DENIRO & EPSTEIN, 1978, 1981). Use of this method in other studies has indicated a trophic link between deep-sea vent bacteria and deep-vent consumers (RAU, 1985; RAU & HEDGES, 1979).

Samples were taken from intertidal vent (*i.e.*, within 10 cm of a vent opening) and non-vent (at least 10 m from